Taxonomic diversity and morphological disparity of paleozoic ammonoids

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Abstract: The Ammonoidea are well represented in terms of numbers of species over a large range of time and they have survived many extinction events. The time interval from the Early Devonian through to the Triassic has seen ammonoid groups evolve and become extinct. The evolutionary history of the Paleozoic ammonoids was punctuated by some extinction events with near extinction events and subsequent recoveries. A Principal Components Analysis (PCA) based on the conch width index (CWI), umbilical width index (UWI) and whorl expansion rate (WER) parameters from 4834 ammonoid species of Devonian to Triassic age produced an empirical morphospace this time interval. The morphospace of Paleozoic ammonoids shows some subtle changes between the periods, but generally, the occupied area is remarkably similar.

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Chapter 16
Taxonomic Diversity and Morphological Disparity of Paleozoic Ammonoids

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16.1 Introduction

Due to their exceptionally diverse and relatively common fossil occurrences, which are global in distribution and their high rates of speciation, Paleozoic ammonoids are ideal organisms for studying regional and global extinction events such as the end-Frasnian Kellwasser events, the late Famennian Hangenberg Event, and the Permian-Triassic Event. The Ammonoidea are also extremely useful to use when tackling questions in paleobiology; measurements and parameters obtained from the conch as well as from their suture lines allow ammonoid researchers to look at morphological disparity and taxonomic diversity. All of these points mean that ammonoid researchers are blessed with an amazing resource with which they can shed light on past events in earth's history.

Diversity and disparity are two ways in which researchers can observe and quantify changes in organismal groups over time. Diversity measures changes in taxonomic units (species, genus or family) between temporal units (period, stage, time bin etc.). Without question diversity estimates of the fossil record can be greatly affected by preservational biases and thus, actual numbers of species are not reflected in the fossil record for a number of reasons (Foote and Sepkoski 1999; Foote 2000). Therefore analyses can give distorted impressions of diversity changes. These

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distortions can be reduced by also looking at morphological disparity (changes in the morphological range), and charting these changes over time, as a taxonomically restrained group may still be morphologically diverse (Villier and Korn 2004). Also by looking not just at changes in species or genus numbers but also at the variation in morphology one can get a more complete idea as to the drivers behind large scale fluctuations in the history of a clade. Since morphology is linked to the lifestyle or *bauplan* of an organism, it reflects how it breaths, eats, moves, etc. So changes in the *bauplan* of an animal group reflect changes in its habits and habitats to some extent.

In this chapter, the taxonomic history and morphological disparity of the Paleozoic Ammonoidea is examined in detail. The changes in both are tracked through many extinction events, some of these events nearly brought about the end of the ammonoids. Recovery periods after extinction events are also of great importance and these are also discussed. There is often a complicated interplay between taxonomic diversity and morphological disparity during the history of the Paleozoic Ammonoidea and that a reduction or rise in one does not necessarily mean the same response in the other. The curves of diversity and disparity may show similar patterns (Hangenberg Event), but may have dissimilar patterns in other cases (e.g., the Kellwasser and Permian-Triassic events). The Paleozoic ammonoids have a discontinuous disparity curve of conch shapes. There was a rapid increase in conch disparity in the Early Devonian, when the Ammonoidea clade was still young, thereafter were periods of high morphological disparity (middle to late Famennian, late Viséan to Bashkirian, Artinskian to Wordian) and low morphological disparity (earliest Famennian, earliest Tournaisian).

The following summary of Paleozoic ammonoid history is largely obtained from the review by Korn and Klug (2012) with the data mainly deriving from the AMMON database (Korn and Ilg 2007) and the inclusion of post-2007 literature.

16.2 Diversity Dynamics of Paleozoic Ammonoids

A key problem when one uses large-scale diversity curves is that chronostratigraphic stages are of unequal length in the Paleozoic (Fig. 16.1); the Wordian is the shortest interval (2.2 Ma) and Viséan the longest (18.9 Ma). There is also an underlying problem, which is linked to the differing number of occurrences that have produced ammonoids from the various stages. To try and address these concerns the species and genus richness per millions of years and per region is also calculated (Fig. 16.1b, c).

In terms of genera and species richness per chronostratigraphic stage, the interval between the Famennian and Bashkirian is the most diverse, with the Famennian represented by more than 700 species and about 150 genera (Fig. 16.1a). However, this changes when the plot illustrating species per millions of years and stage is

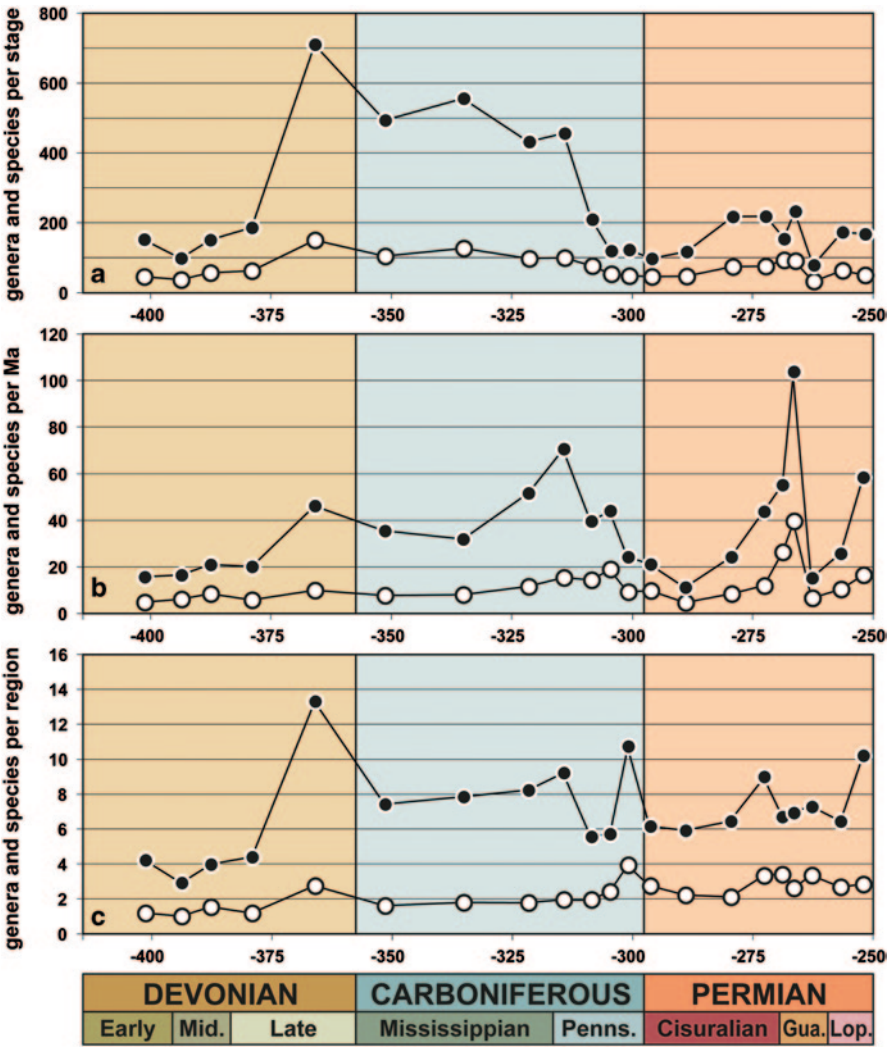

Fig. 16.1 Diversity patterns of Paleozoic ammonoids; data obtained from the AMMON database. **a** Species (*blue dots*) and genus (*white dots*) richness of each stage. **b** Species and genus richness per millions of years in each stage. **c** Species and genus richness per region in each stage (from Korn and Klug 2012)

considered; then, there are several time intervals which are more diverse, namely the Serpukhovian, Bashkirian, Roadian, and Wordian (Fig. 16.1b). When the number of occurrences (regions and areas) is subdivided by the number of species, the Famennian outranks all other stages and stands out in particular when compared with the other Devonian stages (Fig. 16.1c).

16.2.1 Devonian

In the evolutionary history of Paleozoic organisms, the Devonian is a time interval punctuated by several variously severe global events (House 1985, 1989). One of these events, the Upper Kellwasser Event at the Frasnian-Famennian boundary, is one of the so-called 'Big Five' mass extinction events. Although the other Devonian extinction events may not have been as severe, they were still significant global biotic crises (the late Givetian Taghanic Event and the end-Devonian Hangenberg Event). The ammonoids suffered several minor extinctions and almost complete extinctions near the close of the Frasnian and the close of the Famennian, the recovery periods after these events were generally short due to the high speciation rates seen in the Ammonoidea. Korn and Klug (2002) provided an overview of the Devonian ammonoid species and their stratigraphic positions.

The ammonoids originated in the Emsian stage (Early Devonian) from uncoiled or cyrtoconic bactritoids (Schindewolf 1933; Erben 1964). It did not take long for the primitive ammonoids to reach a rather high level in diversity (already from in the early Emsian/Zlíchovian substage, more than 60 species have been described). Locally these primitive ammonoids are abundant and many have a wide geographical range. The richest most diverse occurrences are in Germany (De Baets et al. 2009, 2013), the Czech Republic (Barrande 1865; Chlupáč and Turek 1983), Morocco (Klug 2001a, 2002a), Uzbekistan (Bogoslovsky 1969) and South China (Ruan 1981b). There is a great degree of similarity between many of the species, and therefore the high species number may be an artifact of taxonomic over-splitting (De Baets et al. 2009).

The relatively low number of species (35) in the late Emsian (Dalejan), is most likely explained as a result of the preceding 'Daleje Event' (Ebbighausen et al. 2011). Diversity increased in the next stage (Eifelian) more than doubling to 75 species, followed by a drop in diversity, 55 species, in the early Givetian (the end-Eifelian Kačák Event being the likely driver for this reduction), and 55 in the late Givetian after the Taghanic Event.

These numbers are not absolute, more work must be carried out on the early and middle Devonian time intervals to revise ammonoid taxonomy and as a result of future work, the numbers will undoubtedly change. This is particularly true for the late Givetian, from which assemblages have mainly been documented from Morocco (Petter 1959; Bensaïd 1974; Bockwinkel et al. 2009, 2013).

Diversity increased dramatically in the Frasnian with 200 ammonoid species being described from this stage. However, as in the Emsian, there is a problem with taxonomic practice; the number of species might have been inflated to unrealistic levels due to over-splitting of some of the taxa. One such example of this is seen in the manticoceratid ammonoids (suborder Gephuroceratina) where there are at least 85 species described (Korn and Klug 2002, 2007). These species belong to *Manticoceras* and closely related genera, all within the family Gephuroceratidae. Despite the fact that intraspecific variability in coiling has been known for over a century (Clarke 1899), subsequent authors have neglected to consider this

phenomenon when describing assemblages from various regions. This is particularly true in the case of *Manticoceras*, described by Bogoslovsky (1958, 1969), Clarke (1899), Clausen (1969), Glenister (1958), House and Kirchgasser (2008), Miller (1938), Petter (1959) and Wedekind (1913, 1918). These monographs provide an overview of the putative diversity of the Gephuroceratidae. Even if the morphological range of the genus *Manticoceras* s. str. is reduced, for instance by separation of the oxyconic forms like *Carinoceras* and the more globular ones like *Sphaeromanticoceras*, etc. (as done by Becker and House 1993), there are still more than 40 nominal species left over. The very narrow range of variation in the suture lines and the ornamentation of these nominal species leaves a large question mark over the validity of having so many species (Korn and Klug 2007).

The global Kellwasser Event (end-Frasnian) instigated a drastic reduction in ammonoid diversity (e.g., House 1981, 1985, 1989; Becker and House 1994). The event was two-phased, the first phase (lower Kellwasser Event) reduced the diversity to some degree, and the second (upper Kellwasser Event) brought most groups close to extinction (e.g., McGhee 1988; Buggisch 1991). Apart from the problematic archoceratids (suborder Gephuroceratina), of which the survival into the Famennian has been discussed (Korn et al. 2013a), some lineages of the suborder Tornoceratina survived; they became the root stock from which subsequent ammonoids evolved (Becker 1995).

The Tornoceratina (order Goniatitida) diversified in the early Famennian and were widely distributed along the equatorial and subequatorial shelf regions. The Tornoceratina can be split into two major groups, (1) the 'conservative' tornoceratids with high apertures and (2) the cheiloceratids with modification of the conch towards more globular forms with lower apertures. A total of 220 ammonoid species have been described from the early Famennian, but this number is probably inflated as many are apparently synonyms (see Bogoslovsky 1971 and Becker 1993b for overviews).

The tornoceratids developed a wider and greater variability in morphology during the mid-Famennian; this evolution of new morphologies gave rise to the clymeniid ammonoids (House 1970; Korn 1992; Gottobrio and Saunders 2005) by shifting the siphuncle from a ventral to a dorsal position. This radical change in the ammonoid *bauplan* drove diversity upwards and 260 species have been reported from this interval. Ammonoids of mid-Famennian age have been reported from many regions and the assemblages are generally dominated by clymeniids (e.g., Wedekind 1914; Bogoslovsky 1971; Czarnocki 1989; Nikolaeva and Bogoslovsky 2005). Diversification of Devonian ammonoids reached its height in the mid-Famennian, the *Prolobites delphinus* and the *Platyclymenia annulata* zones; both contain about 100 species each.

There are about 280 valid species known from the late Famennian ammonoid occurrences of Central Europe, the South Urals, North Africa, etc. The Clymeniida were still the dominant order in communities sporting a wide variety of conch geometries, ornament, and suture lines (for an overview see Wedekind 1914; Petter 1960; Bogoslovsky 1981; Czarnocki 1989; Korn and Klug 2002; Nikolaeva and Bogoslovsky 2005).

The Ammonoidea were nearly exterminated by the end-Devonian Hangenberg Event. The upheaval it caused left only two or three of the various ammonoid lineages; one clymeniid lineage survived the event but then rapidly became extinct without leaving descendants (Korn et al. 2004). One goniatite lineage that survived the Hangenberg Event was the basis for all Carboniferous and subsequent ammonoid evolution. Immediately after the event, faunas were extremely low in diversity (approximately 10 species are known so far), composed only of *Acutimitoceras* and closely related forms as well as a few clymeniids (Schmidt 1924; Korn 1984, 1993).

16.2.2 Carboniferous

Shortly after the almost complete extinction of the Ammonoidea during the Hangenberg Event near the Devonian-Carboniferous boundary, a rather sudden increase in diversity occurred. About 100 species are known from the oldest genus zone of the Carboniferous, the early Tournaisian *Gattendorfia-Eocanites* Genus Zone (e.g., Vöhringer 1960; Ruan 1981b; Korn 1994; Bockwinkel and Ebbighausen 2006; Ebbighausen and Bockwinkel 2007). The most diverse assemblages have been found in the Rhenish and Thuringian Mountains, north-western Africa and South China. More than 90% of the ammonoid species of the *Gattendorfia-Eocanites* Genus Zone belong to the subfamily Acutimitoceratinae; its descendants probably gave rise to all subsequent Carboniferous and younger ammonoids.

The middle Tournaisian is the least documented interval of Early Carboniferous ammonoid history; the only records are scattered and rather incomplete (e.g., Miller and Collinson 1951; Gordon 1986; Korn et al. 2002). One of the innovations of this interval was subdivision of the external lobe; this occurred in several independent lineages, it is a nice example of convergent evolution, and was perpetuated by almost all of the Ammonoidea. Konovalova (2005) reviewed the ammonoid diversity dynamics of the Tournaisian; she reported approximately 40 species from the "Middle" Tournaisian (*Goniocyclus-Protocanites* Genus Zone).

For a long time the early Late Tournaisian (*Pericyclus-Progoniatites* Genus Zone) was regarded as a low-diversity period with less then 30 species known. However, after the year 2000 new discoveries from Morocco (Korn et al. 2003), Algeria (Korn et al. 2010a, b) and the eastern United States (Work and Mason 2003–2005) increased the number of species to nearly 100.

The subsequent history of the Early Carboniferous ammonoids is markedly discontinuous; high diversity and low-diversity intervals alternate. The first of these periods is the latest Tournaisian (*Fascipericyclus-Ammonellipsites* Genus Zone), an interval from which approximately 220 ammonoid species have been described from various regions including Ireland, Central Europe, the North Urals, the Tyan' Shan', North Africa and North America (e.g., Holzapfel 1889; Foord 1901, 1903; Librovitch 1927; Delépine 1940, 1941; Schindewolf 1951; Pareyn 1961; Popov 1968; Kusina 1980; Work et al. 2000; Ebbighausen et al. 2010).

After a rather rapid decrease in the early and middle Viséan to about 50–80 species (Riley 1996; Bockwinkel et al. 2010), diversity increased almost continuously toward the latest Viséan to early Serpukhovian. From this interval (Brigantian to Arnsbergian of the British chronostratigraphical scheme), a high number of species has been described: Brigantian: 280 species, Pendleian: 290 species, Arnsbergian: 205 species (see Gordon 1965 for an overview; Ruzhencev and Bogoslovskaya 1971; Ruan 1981a; Korn 1988). It is the most diverse interval within the history of Palaeozoic ammonoids, possibly caused by increasing provincialism connected with the Variscan Orogeny (Korn 1997a; Korn et al. 2012). By far the most diverse occurrences are in the South Urals (Russia and Kazakhstan). Similar, but impoverished assemblages are known from the Cantabrian Mountains of Spain (Kullmann 1961, 1962, 1963), Algeria (Pareyn 1961) and the Anti-Atlas of Morocco (Korn et al. 1999, Klug et al. 2006). Faunas with a different spectrum of genera are known from other areas, for instance the Subvariscan region (Korn 1988, 1997b; Korn and Ebbighausen 2008), the American West (Korn and Titus 2011) and the American Midcontinent (e.g., Gordon 1965).

A combined total of 150 species has been reported from the Chokieran and Alportian (Ruzhencev and Bogoslovskaya 1978) after an extinction event near the Early-Late Carboniferous (Mississippian-Pennsylvanian) boundary. The most diverse assemblages are again from the South Urals, followed by Central Asia. These two regions retained prime importance through subsequent chronostratigraphic units, i.e., Kinderscoutian, Marsdenian, and Yeodonian. From the last unit, 210 ammonoid species are known, suggesting diversity had recovered to about that of the Serpukhovian. Provincialism may be at the root of this high diversity.

Ammonoid faunas from the succeeding stratigraphic units of the Carboniferous are geographically restricted. From the Desmoinesian stage, for instance, ammonoids have been recorded from only a few places in the world, e.g., the American Midcontinent (Oklahoma, Texas), Canada, Japan and Verkhoyan; only about 30 species are known from the Desmoinesian (Boardman et al. 1994).

The late Carboniferous is characterized by the establishment of two regions in which ammonoids are diverse. The first is again the South Urals area (Ruzhencev, 1950); the second is the American Midcontinent (Boardman et al. 1994). It is mainly from these two regions that 100 species are known from the Kasimovian and 120 from the Gzhelian.

16.2.3 Permian

In contrast to the Devonian and Carboniferous, the evolution of the Permian Ammonoidea was not affected by many crises (for a summary see Leonova 2002, 2011). However, the end-Guadalupian and particularly the end-Permian extinction events were severe, of which the latter almost wiped out the entire clade (for a comparison of diversity and disparity, see Villier and Korn 2004; Brayard et al. 2009).

Transition from the Carboniferous to the Permian was not accompanied by a profound faunal change; the evolutionary lineages from the last two Carboniferous stages were also present in the Early Permian. The South Urals and American Midcontinent remain the most important regions from whence Early Permian (Cisuralian) ammonoid faunas have been recorded, supplemented subsequently by faunas from Central Asia and Timor (Haniel 1915; Smith 1927; Miller and Furnish 1940; Ruzhencev 1951, 1952, 1956; Leonova and Dmitriev 1989; Leven et al. 1992). The approximate numbers of species per Early Permian stage are: Asselian 90, Sakmarian 110, Artinskian 210, and Kungurian 215. The increasing diversity during the Early Permian may be explained by the onset of provincialism with vicariance driving evolution in the various regions (American Midcontinent, Urals, Central Asia, South China) and also by the increasing number of ammonoid-bearing localities (species-area effect).

With the disappearance of shelf areas from the South and Middle Urals at the end of the Early Permian, some ammonoid lineages such as the paragastrioceratid and the metalegoceratid ammonoids (order Goniatitida), which are characteristic for that region, declined dramatically. This was probably the reason for the diversity reduction between the Early and Middle Permian (Guadalupian). Only about 140 ammonoid species are known from the Roadian, but thereafter, the earlier high diversity was re-established with a total of 230 species in the ensuing Wordian. Wordian ammonoids were probably the geographically most widespread during the Permian; diverse and similarly composed assemblages are known from Sicily (Gemmellaro 1887, 1888), Timor (Haniel 1915; Smith 1927), Texas (Plummer and Scott 1937; Miller and Furnish 1940), Arctic Canada (Nassichuk et al. 1965) and elsewhere. The Capitanian then saw another reduction in species numbers to less than 100 species.

The Middle-Late Permian (Guadalupian to Lopingian) transition is marked by a selective extinction event (Villier and Korn 2004; Brayard et al. 2009) that particularly reduced the orders Goniatitida and Prolecanitida; conversely, the Ceratitida apparently were enhanced by the event. The Lopingian is dominated by ceratitid ammonoids representing more than 90% of the species diversity (e.g., Zhao et al. 1978; Leonova 2002, 2011). Two independent lineages were present, the araxoceratids (Ruzhencev 1959, 1962, 1963) and the xenodiscids (Shevyrev 1965, 1968). The first of these were particularly common in the Wuchiapingian, the second in the Changhsingian. Both lineages survived into the Triassic, but only the xenodiscids proved successful, forming the rootstock for the Mesozoic ammonoids.

16.3 Morphometric Evolution of Paleozoic Ammonoids

16.3.1 Origin of the Ammonoidea and early Diversification

In the early history of the ammonoid clade in the early Emsian (early Zlíchovian substage), there was a limited occupation of the morphospace. The early coiled ammonoid conchs evolved from the straight conchs of their orthocone ancestors. The

first ammonoid conchs had incomplete coiling and were widely umbilicate (Erben 1964; Klug 2001a; De Baets et al. 2013); this is highlighted by the fact that they are found in one specific area of the WER-UWI scatter plot (Fig. 16.2a; Korn and Klug 2003). From this humble start, the Ammonoidea quickly spread into unoccupied regions of the morphospace thanks to their high evolutionary rates (Fig. 16.2b–f).

There was a rapid development of conch characters in the late Early and Middle Devonian (morphospace filling) followed by a step back from certain morphs, which were presumably of limited success. This led to canalization within the development of ammonoid conchs during this period. Within the early ammonoids, there arose two independent lineages during the late Emsian, which continued through to the late Devonian.

1. The agoniatitid branch (suborders Agoniatitina and Gephuroceratina) is characterized by a rather slow morphological diversification of conch geometry.
2. The anarcestid branch (suborders Anarcestina and Pharciceratina) evolved rapidly and became the rootstock of most of the subsequent Middle and Late Devonian ammonoid clades.

Conch geometry developments in the Early and Middle Devonian ammonoids occurred in three key ways:

- Changes to conch morphology, which was long lasting: this is particularly common in the early ammonoids, for example the Zlíchovian anetoceratids and mimagoniatitids. The long-term shifts that occurred were the increase in the degree of coiling and, as a result of this, a reduction in the size of the umbilical window until it was phased out due to the ammonitella being tightly coiled.
- Short-term changes to conch morphology and character reversals: this is predominantly seen in the anarcestid lineage. Examples of short term trends include the widening of the umbilicus in the anarcestids and then its narrowing in descendant lineages such as the sobolewiids and pharciceratids.
- Character stasis, which is readily observed in the agoniatitid lineage. In other words the conservation of certain conch morphologies such as the *Agoniatites* conch shape.

Morphospaces are widely used in paleontology to order groups of organisms based on their anatomy. Either discrete data or continuous data can be used. Continuous data is the measurements obtained from body parts or shells or better still the ratios of the anatomical feature with respect to body length or shell diameter (Korn 2012). The latter process has been used successfully in ammonoid research for decades ever since the seminal papers by Raup and Michelson (1965) and Raup (1966). Conch measurements have been converted into conch parameters, the most common ones are those known as the Raupian parameters (Raup 1967) or the modified version of the Raupian parameters developed by Korn (2000); it is the ones developed by Korn, which are used in this chapter. The three cardinal conch parameters used are the conch width index (CWI = relative thickness of the conch), umbilical width index (UWI = relative width of the umbilicus) and the whorl expansion rate (WER = coiling rate of the whorl spiral) (Korn 2000).

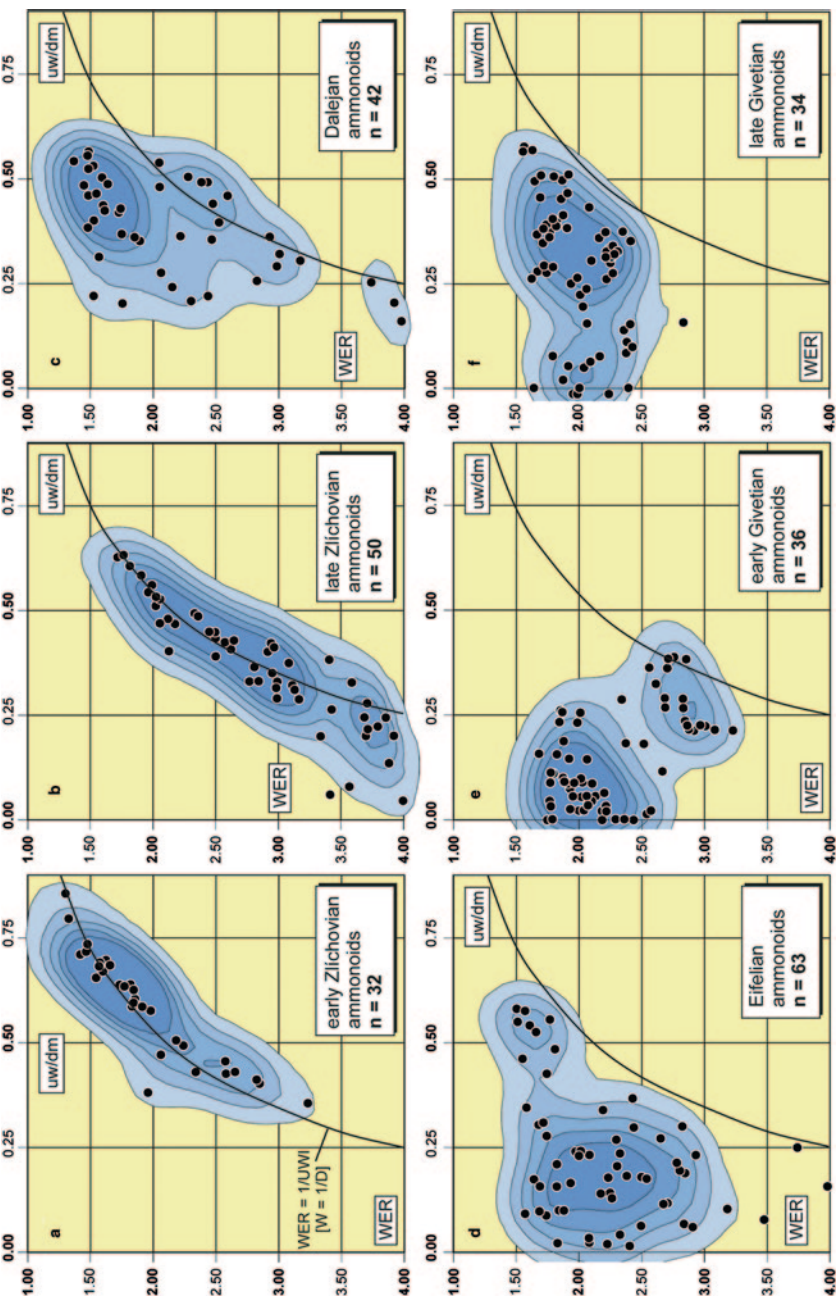

Fig. 16.2 Bivariate plots showing the morphospace occupation of the cardinal conch parameters (WER and UWI) are pair-wise illustrated for six successive Early and Middle Devonian time intervals (from Korn and Klug 2012)

It is a combination of the changes to the parameters, which shapes the conch of an ammonoid. Species that have a high WER show impressive changes in conch diameter and aperture height over just a small number (ca. 5–8) of whorls. Such forms have relatively short but high body chambers, whereas ammonoids with a low WER have long but flattened body chambers (Okamoto 1996; Klug and Korn 2002). Individuals that have a high CWI possess conchs that are rather globular in appearance, and those conchs with a low CWI, are discoidal. Widely umbilicate ammonoids (high UWI) had relatively large umbilical openings. These three cardinal conch parameters have a pronounced effect on the overall conch form, and it is for this reason that they are often used to express morphospaces either in the form of bi-plots or Principal Components Analysis (PCA). An analysis of measurements and their ratios taken from the last intact whorls of ammonoids allows researchers to track any significant changes in the distribution of the data points within a morphospace over time (e.g., Saunders and Swan 1984; Dommergues et al. 2001; Korn and Klug 2003; Klug et al. 2005; McGowan 2007; Moyne and Neige 2007; Saunders et al. 2008; Simon et al. 2010, 2011).

16.3.2 Conch Morphology of Devonian Ammonoids

In the Paleozoic, the greatest range of ammonoid conch morphologies was found in the Devonian. This can be explained by the fact that the Ammonoidea originated in this period, and there was a rapid origination of new and novel conch morphs not previously seen in the Paleozoic (Korn 2000, 2001; Korn and Klug 2002, 2003). Indeed, it has been shown for a number of different animal groups that morphological disparity often reaches a maximum relatively early in a clade's history (Foote 1994; Wills et al. 1994). Also, in this early period of ammonoid evolution, some conch morphologies were quickly replaced by newer forms relegating them to obscurity. These 'defunct' forms, which were replaced, were for a short period novel and competitive. Additionally, these were important stepping-stones to more tightly coiled conch morphs with improved hydrodynamic properties (Klug and Korn 2002). Openly coiled conchs are a good example of such a linkage form; they evolved from the straight conchs of the orthocones (De Baets et al. 2013). Additionally, they were obviously more tightly coiled than their predecessors and profited from the greater mobility and as such could occupy new habitats. However, conch evolution continued into the late early Devonian, resulting in more and more tightly coiled ammonoids that probably enhanced greater mobility. As a result of this process, more primitive openly coiled conchs became from an evolutionary perspective less competitive and eventually extinct. Therefore, these conch forms are only found in the Devonian (when concerning only the Paleozoic), leaving an area of ammonoid conch morphospace, which remains empty or only partially filled in proceeding time intervals in the Palaeozoic. Two major ammonoid clades occurred early in the late Emsian (Dalejan) faunas, which had significant differences in conch shape and conch ontogeny. These are

the suborders Agoniatitina and Anarcestina (Klug 2002b; Korn and Klug 2002). A characteristic of the agoniatitids is their conservative morphology, which is similar to the ancestral mimagoniatitids (particularly in the laterally compressed subinvolute conchs with a high aperture). The anarcestids had a rapid development towards evolute conchs with a low aperture and a ventrally depressed whorl cross-section.

Differences in the adult conch morphology are also manifested in the ontogenetic trajectories of the main conch parameters. The trajectories can be separated into phases; phases are time intervals that show a certain common trend. The trend can be an increase in a conch parameter or a decrease or increased period of relative stability. Ontogenetic trajectories can thus be described according to the number of phases that they possess, monophasic (one phase), biphasic (two), triphasic (three) and polyphasic (more than three). Similarities in the plots of ontogenetic trajectories such as number of phases, direction of change and extremity of the change can be seen between related groups of ammonoids. This can help ammonoid researchers to infer phylogenetic relationships between different clades; this was the case with the agoniatitids and the gephuroceratids (Korn 2001; Korn and Klug 2001, 2002).

The morphometric analysis of approximately 700 Early Devonian to Early Tournaisian ammonoid (Fig. 16.3) species shows large-scale patterns. Particular interest was paid to the CWI, UWI and the WER. These parameters were computed according to the study by Korn (2000) (compare also Raup 1967).

A PCA was carried out on the data from the three cardinal conch parameters, and a triangular morphospace was plotted based on the results of the PCA (Fig. 16.4). The first two axes of the PCA explain a total of almost 90 % of the variance within the sample (PC1 = 52.6 %; PC2 = 36.9 %). Variations along PC1 are mainly associated with the shape of the body chamber (factor loading: CWI = −0.925, UWI = 0.710, WER = 0.469); PC2 depends mainly on the whorl expansion rate and the umbilical width index (CWI = −0.054, UWI = −0.626, WER = 0.843).

The earliest ammonoids were loosely coiled and had wide umbilici as well as low WERs (anetoceratids); they plot in the bottom to middle right of the morphospace (early Zlichovian). There is a change from these early forms to conch forms (mimagoniatitids), which are more involute and which also possess higher apertures (late Zlichovian to Dalejan), seen by an upwards trend in the data plots and a move to the center (Fig. 16.5).

In the Eifelian the anetoceratids are no longer present (a trimming of the right margin), and despite an extension of the occupied area of the morphospace towards the left there is an overall reduction in the sum of range (SOR).

There is a more extensive trimming of the margins in the early Givetian, resulting in a smaller occupation of the morphospace. The early Givetian has the lowest SOR of all the Early and Middle Devonian intervals (Fig. 16.5) and therefore represents a low disparity period in the evolutionary history of the ammonoids. There is no major transition event of conch forms between the early and late Givetian. Conch morphology, as controlled by the three cardinal conch parameters, was

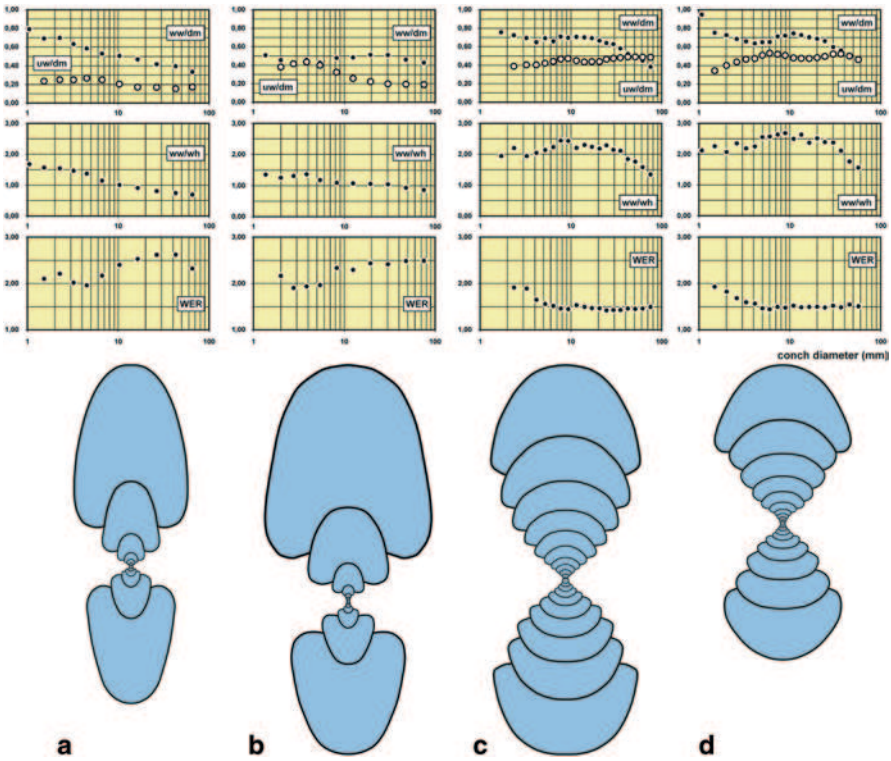

Fig. 16.3 Ontogenetic development of conch geometry in some Devonian ammonoids (Korn and Klug 2001, 2007; Klug 2002a). The diagrams represent (from *top to bottom*) development of the conch width index (ww/dm), umbilical width index (uw/dm), whorl width index (ww/wh), and whorl expansion rate (WER). **a** *Fidelites clariondi* (Petter 1959). **b** *Manticoceras* sp. **c** *Sellanarcestes wenkenbachi* (Kayser 1884). **d** *Pharciceras* sp.

mostly unaffected by the Taghanic Event. although there is an influx of more widely umbilicate forms (morph A) in the late Givetian.

16.3.3 Devonian Extinction Events

The time interval from the Emsian (Early Devonian) to the early Tournaisian (Early Carboniferous) includes a number of geological events (Table 16.2). These events are defined primarily by punctuations in the diversity history of the Ammonoidea (e.g., House 1985, 2002; Walliser 1985, 1996; Table 16.1).

As can be seen from Table 16.2, not every geological event had a discernible effect on the ammonoid conch-shape record (Fig. 16.5). The three events, which had the biggest impact were the Kačák, Upper Kellwasser and Hangenberg events (Fig. 16.6).

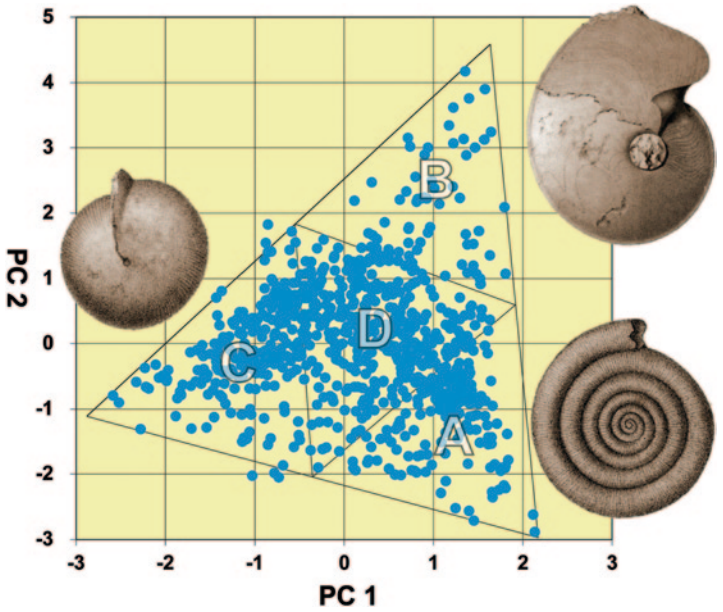

Fig. 16.4 Empirical morphospace of the Devonian ammonoids calculated using the three conch parameters WER, CWI, and UWI, together with representative examples (morphs) of ammonoids and their position within the morphospace segment (from Korn and Klug 2012)

16.3.4 Kellwasser Crisis and Recovery

There was almost no fluctuation in morphological disparity between the late Givetian and the mid-Frasnian; the 'Frasnes Event' is not apparent when one regards ammonoids (Fig. 16.6). In fact, this event, rather than having a negative effect on ammonoids, could be seen as having a positive effect if one looks at species numbers. There is a minor shift towards forms with a high aperture and narrow umbilicus (morph B) in this interval. The margins of the morphospace are reduced as a result of the Lower Kellwasser event resulting in a decrease in disparity. At the same time, some widely umbilicate forms (morph A) reappeared. Morph B is the dominant form; this is due to the evolutionary peak in gephuroceratids. However, morph A does reappear at this time. The disparity measures are inconsequential; the sum of range decreases markedly but the sum of variance is stable (Fig. 16.6c, d).

The Upper Kellwasser Event (Frasnian–Famennian boundary) was a major extinction event for the Ammonoidea (Becker et al. 1989, 1993; Becker and House 1994). The suborder Gephuroceratina became almost extinct and as a result of this, Morph B, which is extensively represented by the suborder, collapsed. If *Archoceras* managed to survive the Kellwasser Event as the last surviving member of the gephuroceratids, it was only the last gasp of the family as they produced no descendants, i.e., a 'Dead Clade Walking' according to Jablonski (2002) or 'failed

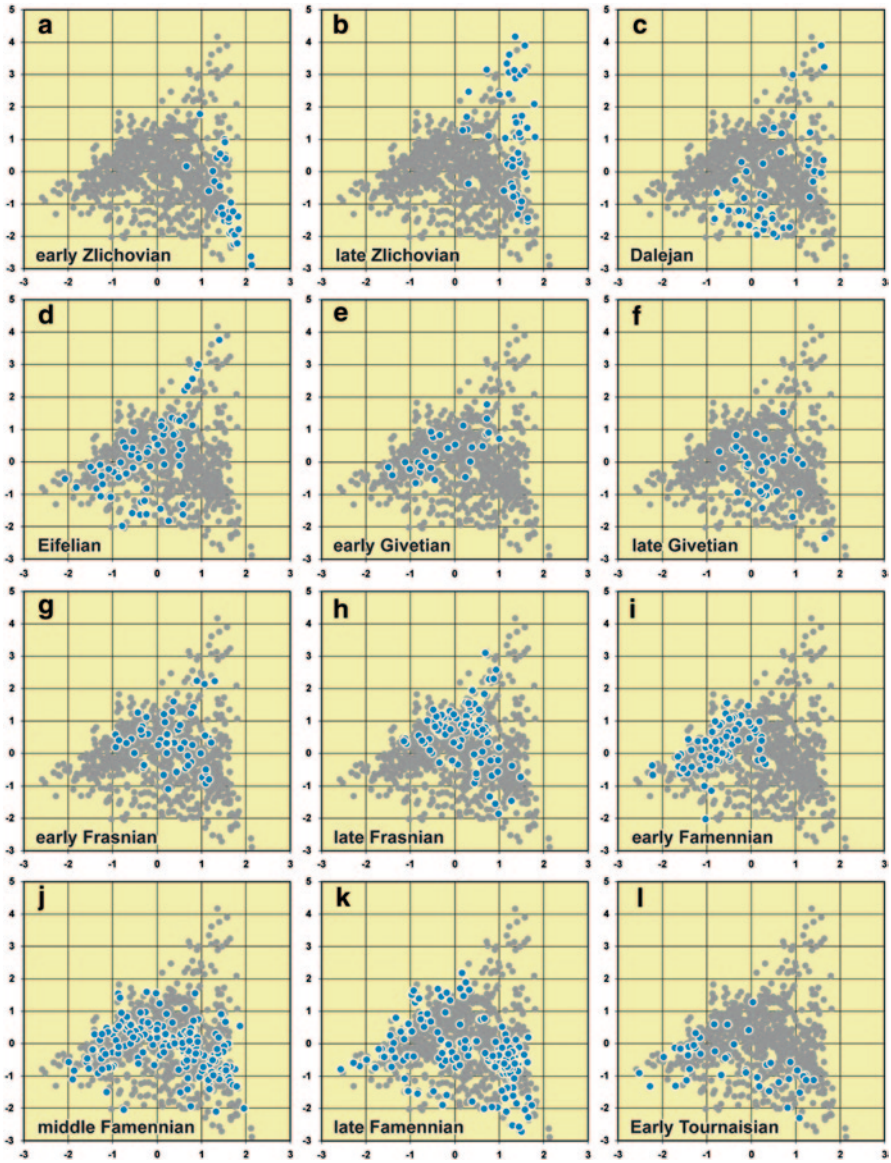

Fig. 16.5 Morphospace occupation of Early to Late Devonian ammonoids and the transition into the earliest Carboniferous by application of the method of a principal component analysis (using conch parameters whorl expansion rate, conch width index, and umbilical width index). From Korn and Klug (2012). *Big circles* are the values from the respective interval, while the *small dots* show values from the entire Paleozoic

survivor' according to Korn et al. (2004). As with the Lower Kellwasser Event, only the sum of range is profoundly affected (and also the range of the middle two quartiles of the occupied morphospace), but the sum of variance is stable.

Table 16.1 Conch characters of the analyzed Devonian ammonoid suborders (Fig. 16.3)

Suborder	Defining characters of the conch ontogeny
Agoniatitina (Emsian to Givetian)	The conch ontogeny is strongly influenced by changing rates of coiling. *Fidelites* (Fig. 16.3a) has a low aperture in the juvenile period (WER = 2.00), there then follows a period (preadult) with an acceleration of the coiling rate, which is then followed by stagnation in the adult stage. There is a strong resemblance to the coiling rates seen in the mimagoniatitids, an in depth analysis of the genus *Rherisites* has been carried out by Klug (2001b)
Gephuroceratina (latest Middle Devonian and Frasnian)	Changes in the WER are quite similar to those seen in the Agoniatitina, although the adult conch shapes can differ. *Manticoceras* for example has a similar conch shape to *Fidelites* and shares the postembryonic tripartite ontogeny in the WER (Fig. 16.3b). Close phylogenetic relationships between the agoniatitids and the gephuroceratids have been proposed due to the strong resemblance of their conch ontogenies and the similar sizes of their ammonitella (Korn 2001, Korn and Klug 2001, 2002)
Anarcestina (Emsian to Givetian)	They are characterized by an ontogeny, which shows only minor changes in the main conch parameters. The CWI and WWI are relatively stable over long periods of growth (Fig. 16.3c), in the example specimen the UWI increases continuously but slowly, the aperture remains low throughout the entire growth period (Klug 2002a)
Pharciceratina (Givetian and early Famennian)	These multilobate ammonoids possess a conch ontogeny comparable to that of the anarcestids (Fig. 16.3d). Despite developing an increased variation in conch morphology, their ontogenetic trajectories closely resemble Emsian to Eifelian anarcestids. Our example (*Pharciceras*) virtually shows the same conch ontogeny as *Sellanarcestes*. Advanced pharciceratids differ from our example in having a closed umbilicus, but the ontogeny of their coiling rate is still characteristic for the anarcestid–pharciceratid lineage (Korn 2001). The main difference from their anarcestid ancestors is the increase in sutural complexity in pharciceratids (Saunders et al. 1999, 2008; Korn and Klug 2002)

There was a slow recovery after the Upper Kellwasser Event in the early Famennian ammonoid zones. The Tornoceratina survivors suffered a severe reduction in their morphospace occupation. In the early Famennian, however, the cheiloceratids diversified and managed to fully occupy the area of morph C, a first in the history of the ammonoids. The empty space resulting in the loss of the gephuroceratids was not filled for about 8 Ma; it was not until the mid-Famennian (*Pernoceras dorsatum* and *Pseudoclymenia pseudogoniatites* Zones) that parts of this area were repopulated by the tornoceratids. This instigated a change in morphospace occupation and House (1985) named this the ‘Nehden Event’. Nevertheless, this event should be interpreted more as an innovative period in the evolution of the tornoceratid ammonoids rather than as a crisis.

The *Prolobites delphinus* Zone saw the introduction of the clymeniids, and with this rapidly diversifying group, the ammonoids reached a point of recovery after the devastation of the Upper Kellwasser event. Indeed, a peak in morphological range can be seen at this point. There is no true innovation in conch forms by the tornoceratids and cheiloceratids; they maintained their morphospace occupation (mainly

Table 16.2 Devonian geological events and their effect on ammonoid evolution

Devonian geological events	Effect on ammonoid morphology
Daleje Event	Disappearance of crioconic shells
Choteč Event (close to the Emsian–Eifelian boundary)	Disappearance of the umbilical window in the embryonic shell
Kačák Event (close to the Eifelian–Givetian boundary)	Major effect on ammonoid evolution seen by a reduction in occupied area of morphospace (SOR is reduced)
Taghanic Event (mid-Givetian)	Minor extinction event, but with recovery and dispersal of surviving lineage (pharciceratids)
Frasnes Event (Middle–Late Devonian boundary)	No discernible effect on the Devonian ammonoid morphospace
Lower Kellwasser Event (late Frasnian)	Minor extinction event, but with recovery and dispersal of surviving lineage (archoceratids)
Upper Kellwasser Event (Frasnian–Famennian Boundary)	Major effect on ammonoid evolution seen by a reduction in occupied area of morphospace (SOR is reduced)
Enkeberg Event (early Famennian)	No discernible effect on the Devonian ammonoid morphospace
Annulata Event (middle Famennian)	No discernible effect on the Devonian ammonoid morphospace
Dasberg Event (late Famennian)	No discernible effect on the Devonian ammonoid morphospace
Hangenberg Event (close to the Devonian–Carboniferous Boundary)	Major effect on ammonoid evolution seen by a reduction in occupied area of morphospace (SOR is reduced), almost the entire morphospace range was affected

morph C); the clymeniids quickly diversified spreading over a wide range in the morph A and morph D areas.

The Annulata Event and the Dasberg Event had no discernible effect on the morphometric evolution of the Ammonoidea (Becker 1993a), which can be seen by a lack of any major difference in the disparity indices over the following zones (Fig. 16.6c, d). In the middle *Wocklumeria* Stufe, the clymeniids instigated a marked change in the occupation of the morphospace by dispersing over most of the morph A field and evolving conch forms similar to goniatitid morphology (morph C).

16.3.5 Hangenberg Event and its Aftermath

The Hangenberg Event had the biggest impact on the Ammonoidea out of all of the Devonian extinction events (Korn 1993, 2000; Korn et al. 2013b). As a result of the massive loss of species, especially in the Clymeniida and the Goniatitida, there was a dramatic drop in taxonomic diversity and morphological disparity. The survival of a few clymeniid species produced no descendant species, and the lineage terminated

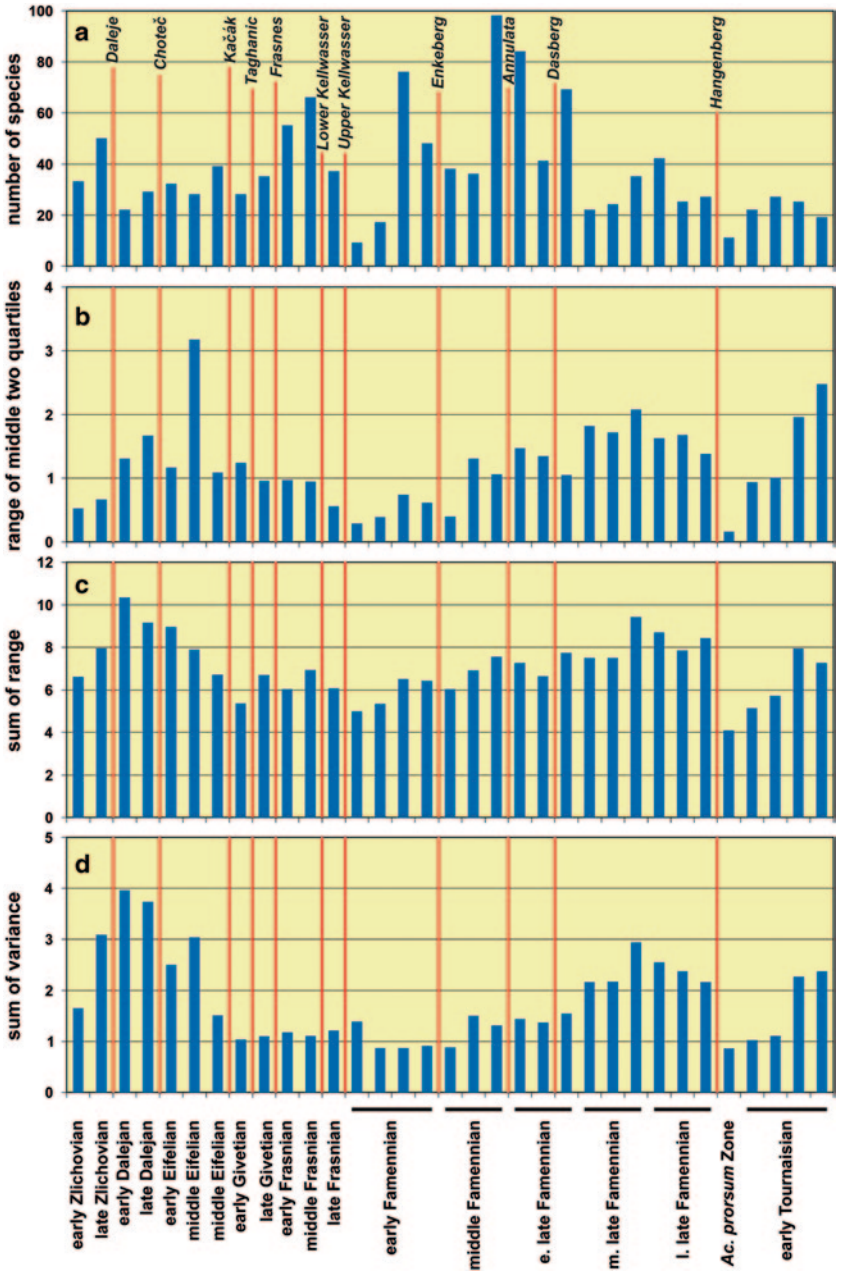

Fig. 16.6 Diversity and disparity fluctuations of Early to Late Devonian ammonoids and the transition into the earliest Carboniferous illustrating the impact of the various geological events (from Korn and Klug 2012)

shortly after the extinction event (Korn et al. 2004). One goniatite lineage, the Goniatitida, survived the Hangenberg Event and managed to flourish in the new world order filling niches that were once occupied by the clymeniids.

Before the Hangenberg Event, in the *Wocklumeria sphaeroides* Zone, the ammonoid morphs (A-D) were all represented, albeit in a dispersed manner. The Hangenberg Event affected all morphs; there was a drastic reduction in the sum of range and sum of variance evident in the post-event *Acutimitoceras prorsum* Zone. The goniatites conch morphology is rather restricted and therefore plots in a narrow area in the morphospace (Fig. 16.7).

A partial refilling of areas in the morphospace, vacated by the clymeniids and tornoceratids, occurred over the following Carboniferous *Acutimitoceras acutum* to *Paragattendorfia patens* Zones. However, the range of morphospace occupation during the Early Tournaisian did not reach previous levels found in the Late Devonian.

16.3.6 The Basal Carboniferous Recovery

Morphometric analyses of Carboniferous ammonoids have been undertaken several times (Saunders and Swan 1984; Nikolaeva and Barskov 1994; Saunders and Work 1997; Saunders et al. 1999). Previous stratophenetic studies of the ammonoid assemblages from the latest Devonian to earliest Carboniferous cephalopod limestone succession of the Rhenish Mountains (Korn 1986, 2000) revealed some telling changes in the morphological evolution of the Ammonoidea. The investigation concentrated on the WER and the UWI, two conch characters, which are very important in ammonoids since they indicate body-chamber length (and hence orientation in the water column) and mobility as well as the shape of the body chamber. The main findings were that the Hangenberg Event caused an almost complete change in the morphological spectrum adopted by ammonoids. As already stated, the clymeniids and tornoceratids became extinct at or immediately after the Hangenberg Event; the morphospace area they once occupied was refilled by the surviving prionoceratid ammonoids (Fig. 16.7), albeit not completely.

Although the Hangenberg Event was devastating, there was a rapid rate of recovery afterwards; eight species of prionoceratids, with an open umbilicus in their juvenile stage are present in the latest Devonian *Acutimitoceras prorsum* Zone, which is the first post-event zone. *Acutimitoceras* and *Nicimitoceras* seem to appear in next to no time with a new conch geometry, which was probably developed earlier.

There was no major increase in conch diversity over the four earliest Carboniferous zones from the *Acutimitoceras acutum* Zone to the *Paragattendorfia patens* Zone (Fig. 16.8). A group of widely umbilicate goniatites became well established, but intermediates were not important as can be seen by their absence.

It is remarkable that the goniatites of the '*Gattendorfia* Stufe' differ so conspicuously in their WER/UWI proportions from the clymeniids of the Late Devonian '*Wocklumeria* Stufe'. The bivariate plot of the WER/UWI values of all the clyme-

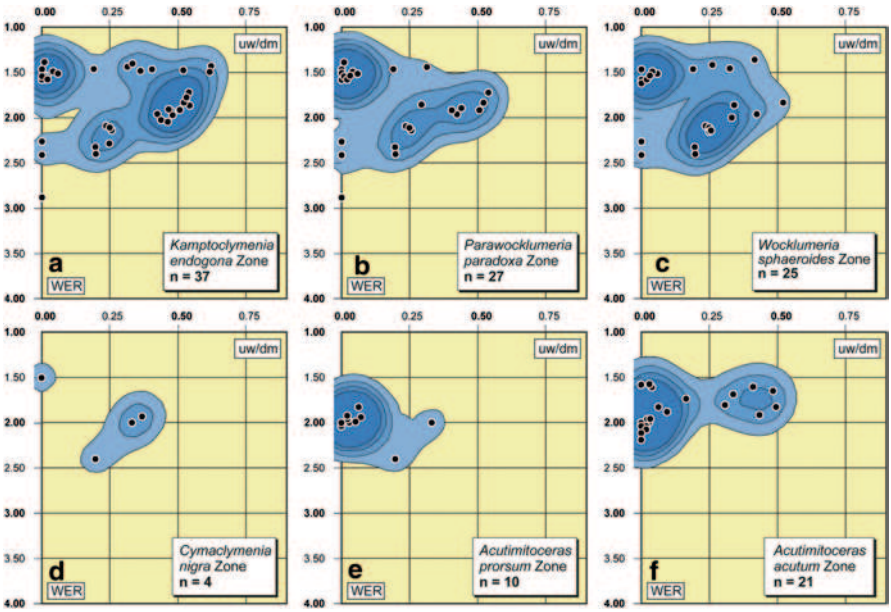

Fig. 16.7 Morphospace occupation using the example of WER–UWI couplet across the Devonian-Carboniferous Boundary (after Korn 2000). Note the sharp decrease in the *Cymaclymenia nigra* Zone (Hangenberg Event) and the subsequent recovery

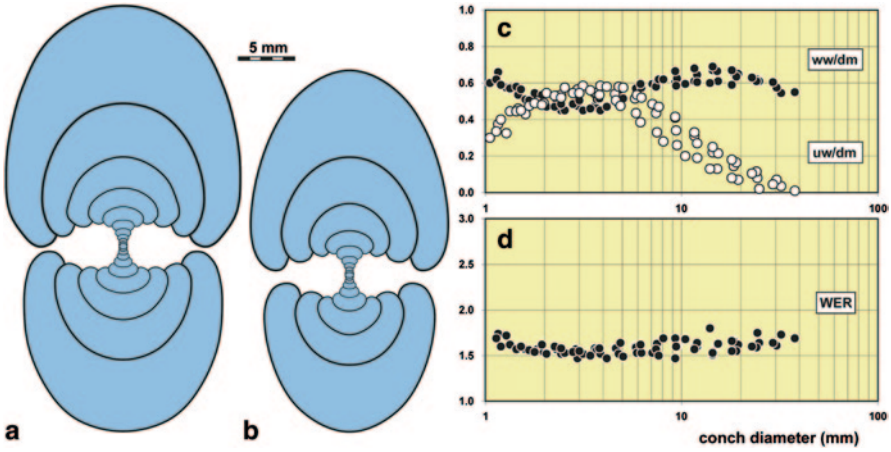

Fig. 16.8 Conch ontogeny of the latest Devonian *Acutimitoceras hilarum* Korn, 2004 from Lalla Mimouna (Anti-Atlas, Morocco) on the basis of cross-sections. **a, b** Cross sections, x 2.0. **c** Ontogenetic development of the whorl width index (ww/dm) and umbilical width index (uw/dm). **d** Ontogenetic development of the whorl expansion rate (WER)

niids from the '*Wocklumeria* Stufe' and goniatites from the '*Gattendorfia* Stufe' demonstrates the significant differences in position of the morphospace occupied by these groups (Fig. 16.7).

16.3.7 Conch Morphology of Carboniferous Ammonoids

Nearly all Carboniferous ammonoids can be assigned to a single monophyletic clade, which originated in the earliest Tournaisian prionoceratids. This clade gave rise to two subclades, the Carboniferous and Permian representatives of the Goniatitida and the Prolecanititida. The genus *Acutimitoceras* is a good candidate for being close to the initial radiation of the two subclades; its conch ontogeny has been intensively studied (Bockwinkel and Ebbighausen 2006) on the basis of material from the Rhenish Mountains and the Anti-Atlas.

Acutimitoceras hilarum is a Late Devonian species with strikingly allometric conch growth and can thus be used as a characteristic example for many Carboniferous and Permian ammonoids (Korn et al. 2004, 2007). Its conch ontogeny consists of three stages, which are mainly driven by changes in the proportions of the whorl width (a triphasic ontogenetic trajectory) and by a biphasic change in the umbilical width (Fig. 16.8). The first growth stage (which may be called serpenticonic) is characterized by slowly expanding, ventrally depressed whorls embracing the preceding whorl to a minor degree only. During the second stage, the whorl cross-section becomes more circular and increasingly embraces the preceding volution; as a result of these changes, the conch developed a stouter form. The adult stage is marked by an almost complete closure of the umbilicus and lateral compression of the whorls.

Korn and Vöhringer (2004) analyzed the ontogeny of *Gattendorfia crassa* from the early Tournaisian (Mississippian) Hangenberg Limestone of the Rhenish Mountains. It is well placed, due to its basal position in the Carboniferous ammonoids, to be used as a model for many lineages. There is a general similarity between the ontogenies of *Gattendorfia* and *Acutimitoceras*, with the obvious exception that the umbilicus is not completely closed off in the adult stage of *Gattendorfia*. The conch ontogeny closely resembles that of other Carboniferous species, such as *Cravenoceras leion* from the basal most Serpukhovian strata of Derbyshire, in which the adult morphology as well as several ontogenetic trajectories are similar to *Gattendorfia* (Korn and Tilsley 2002). The ontogenetic changes affecting the outline of the whorl cross-section are striking; this reflects a rearrangement of soft parts in the body chamber of the animal.

The aforementioned examples can be regarded as ontogenetic models for many of the Carboniferous ammonoids, which usually possess a triphasic postembryonic conch ontogeny. The three phases can, however, show a remarkable degree of variability in the strength of the expression and in their length.

16.3.8 Permian Extinction Events

Using the four cardinal conch parameters (WER, UWI, WWI and IZR), Villier and Korn (2004) ran a PCA and plotted an empirical morphospace for Permian and earliest Triassic ammonoids (Fig. 16.9). The resulting scatter plot resembles that of the Devonian ammonoids in its triangular field. The major conch morphologies, of this time interval are pictured (Fig. 16.9):

- Morph A—represented by *Paragastrioceras* (with a widely umbilicate, slender conch and low coiling rate);
- Morph B—represented by *Artinskia* (with a narrowly umbilicate, slender conch and high coiling rate);
- Morph C—represented by *Almites* with a narrowly umbilicate, globular conch and low coiling rate).

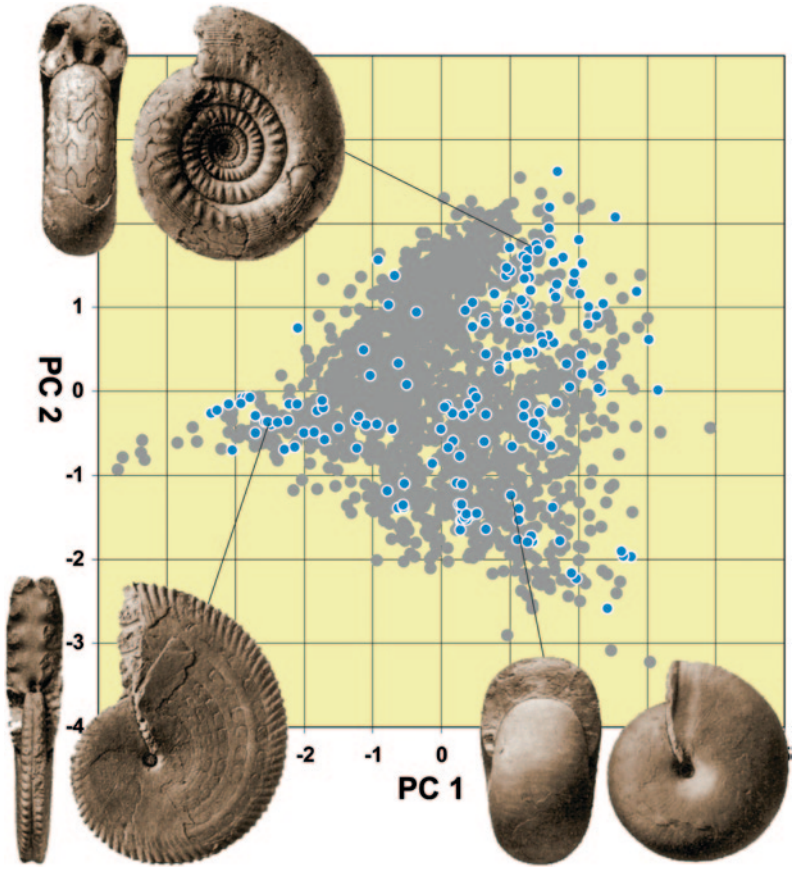

Fig. 16.9 Morphospace occupation using conch parameters: whorl expansion rate, umbilical width index, whorl width index, and imprint zone rate of the ammonoids from the latest Carboniferous to Early Triassic. After Villier and Korn (2004). Examples of the extreme morphologies are shown at the sides of the morphospace triangle

The disparity indices sum of variance and sum of range were calculated from the empirical morphospace. The temporal changes in disparity (variance and range) generally follow the pattern of the diversity curve for superfamilies, but at low taxonomic levels, diversity and morphological disparity are independent. There was an increase in disparity from the Late Carboniferous to the Early Permian. It then remained relatively stable for the first three stages of the Permian. From the Artinskian to the end of the Permian (approximately 30 Ma), there is a general decreasing trend in disparity; this is briefly interrupted by an increase in the Wordian. There is a substantial difference in the patterns of the two disparity estimates; fluctuations in variance are more pronounced, whereas the decreasing trend of the range occurs more regularly. Due to their diversification, an increase in the disparity of three groups (Neoicoceratacеae, Adrianitaceae, and Cyclolobina) helped to drive the brief increase that is observed in the Wordian. The end-Capitanian crisis is characterized by the loss of a large number of genera (Glenister and Furnish 1981). The downward trend in disparity continued during the two last stages of the Permian; the lowest value occurred just before the end-Permian mass extinction in the Changhsingian. The early Triassic is marked by stagnation in variance and only the morphospace occupation increased.

The end-Capitanian and the end-Changhsingian are two distinct mass extinction events, the latter standing out due to its intensity. There are three major patterns to be seen in the morphological disparity through time of the Permian ammonoids: a long-term reduction in disparity, a high level of selective extinction at the end of the Capitanian, and a non-selective extinction at the end of the Permian (Korn et al. 2013c). The end-Capitanian event shows, despite the high level of extinction, a pattern that corresponds to a model of background extinction. The pattern of the end-Permian extinctions are in agreement with the model of a ‘mass extinction regime’ (Jablonski 1986, 2005), consisting of a major event, which is relatively brief in duration, has a global effect, is independent of earlier variations in diversity, and which is random in nature in terms of the taxa, which are killed off.

16.4 Ammonoid Morphospace Over the Paleozoic and Triassic

The Paleozoic and early Mesozoic represents an interesting interval in the history of the Ammonoidea; it contains not only the origin of the Ammonoidea but it also includes numerous extinction and diversification events. These periods of evolutionary upheaval will be reflected in the development of the ammonoids and are best seen in the changes that occur to their suture lines and conch shapes. The three cardinal conch parameters provide an excellent basis on which to analyze the changes in conch morphology. A Principal Components Analysis (PCA) based on the CWI, UWI and WER parameters obtained from the last measurable half whorl of 4834 ammonoid species from the Devonian through to the Triassic was performed (Fig. 16.10). The first two principal components explain 85.5% of the

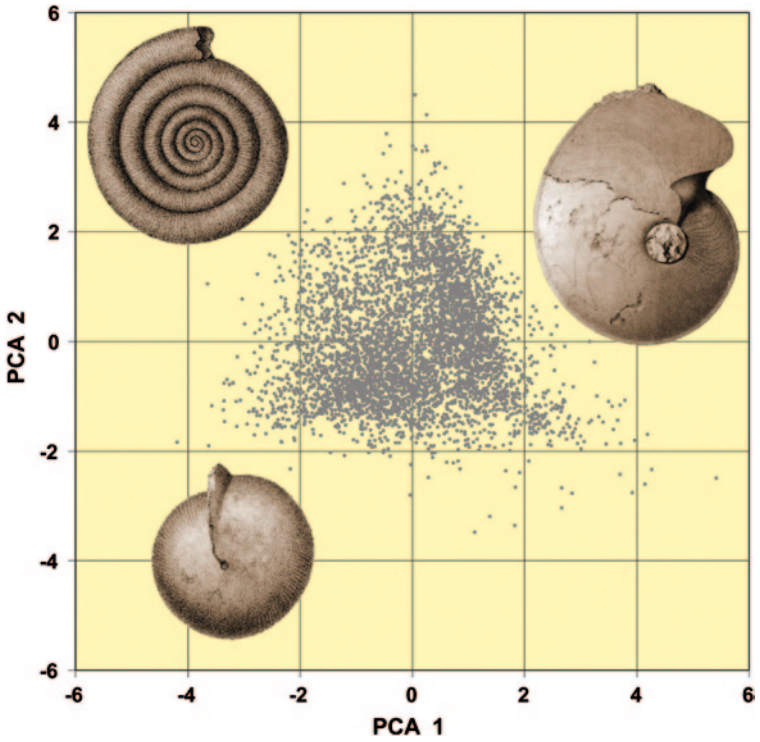

Fig. 16.10 The occupation of morphospace analyzed by a principal components analysis of the cardinal conch parameters conch width index, umbilical width index and whorl expansion rate. Examples of the extreme morphologies are shown at the sides of the morphospace triangle

Table 16.3 The disparity indices, sum of variance, sum of range and range of the middle two quartiles (RMQ) in the Principal Components Analysis of the morphometric data from Devonian to Triassic ammonoids

PC	Eigenvalue	% variance
1	1.387	46.23
2	1.177	39.25
3	0.436	14.52

variance (Table 16.3). The disparity indices, sum of variance (SOV), sum of range (SOR) and range of the middle two quartiles (RMQ) were calculated for the first two principal components for each of the four periods (Table 16.4).

The filled area of the morphospace for all of the specimens is triangular in shape, with the three end points representing extreme morphotypes (Fig. 16.10). In order to see the differences in morphospace occupation over the time periods, the data points for each period are plotted against the complete dataset.

The Devonian shows a high density of taxa on the right side of the total occupied morphospace. There are a number of specimens in the bottom right point of the

Table 16.4 Disparity indices of the first two principle components of the analyzed time intervals

Period	SOR	RMQ	SOV
Devonian	15.16	3.31	2.73
Carboniferous	12.41	2.75	2.07
Permian	13.44	3.51	2.75
Triassic	14.15	2.89	2.06

SOR sum of range, *RMQ* range of the middle two quartiles, *SOV* sum of variance

triangle, representing more extreme conch forms which are sub-involute, discoidal and with very high WER values. Another extreme conch form also represented is in the top point of the triangle. These morphs are very evolute, extremely discoidal and have a very low WER (Fig. 16.11a). The Devonian has a high range in disparity, both overall and in the RMQ. This is representative of the fast evolutionary rates of the Ammonoidea, showing how they quickly radiated not just in terms of number of species but also in terms of morphological disparity. With the second highest variance, the Devonian also represents a time with less clustering around a small number of conch morphs (Table 16.4).

There is a dramatic change between the positions of the Carboniferous taxa with that of the Devonian; the Carboniferous species populate mainly the left and middle of the empirical morphospace with a marked move away from the area representing the two conch morph forms mentioned above (Fig. 16.11b). The large shift in morphospace occupation was probably instigated by the mass extinction events that took place at the end of the Devonian, especially the Hangenberg Event. The densely populated areas of the Carboniferous morphospace are representative of ammonoids with globular and pachychonic conch forms they are sub-involute and with low apertures. The Carboniferous has the smallest SOR out of all of the periods at 12.41. This reflects the reduction in the morphospace occupation especially with the absence of any species in the more extreme morph ranges around the top and bottom right points of the empirical morphospace triangle. A low variance value also matches the changes in conch forms as there is a reduction in the variety of conch morphs in this period of ammonoid evolution (Table 16.4).

The changeover from the Carboniferous to the Permian is not marked by a major ammonoid extinction event as is indicated by the fact that there no dramatic changes in morphology at the boundary of the two periods (see Figs. 16.7 and 16.11). The area occupied during the Carboniferous is still filled in the Permian, although not as densely. There is an increase in taxa towards the far right of the overall morphospace, which was unoccupied in the Carboniferous. More species are now seen again in the morphospace area in the bottom right. In the Permian there is an increase in the RMQ, it reaches its highest value of 3.51, and the SOV also reaches its highest level at 2.75 (Table 16.4). This shows a return to taxa being more spread around a greater number of conch morph forms, as was seen in the Devonian.

The Permian-Triassic mass extinction event hit the Ammonoidea hard. Only a few genera survived this period of instability, and this explains the massive reduction in globular ammonoid conchs and the abandonment of the extreme left side of

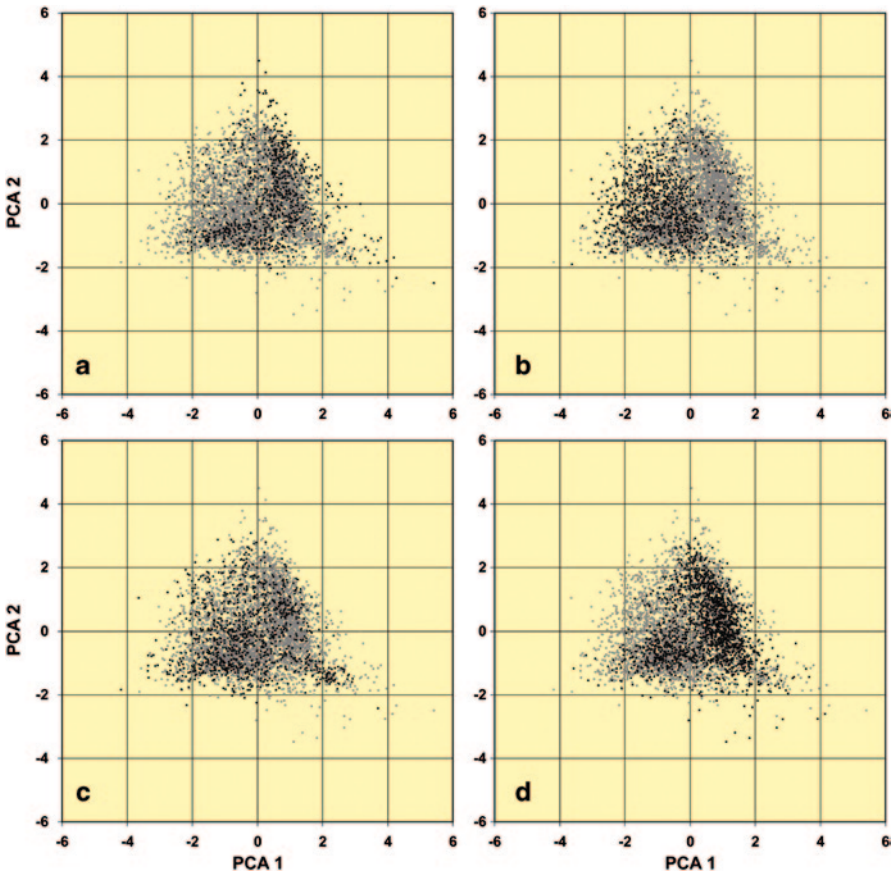

Fig. 16.11 Changes in the occupation of ammonoid morphospace through time **a** Devonian, **b** Carboniferous, **c** Permian and **d** Triassic ammonoids

the overall morphospace area in the Triassic plot. The RMQ is greatly reduced from that of the Permian, and the variance is the lowest of all four periods, this shows another move towards a strong concentration on a reduced number of conch morph forms similar to the Carboniferous, but this time towards narrower conchs (discoidal) with high apertures (WER = 2.00 − 2.50).

16.5 Conclusions

When looking at the extinction and diversification patterns of ammonoids during the Paleozoic, it is not enough to look solely at the taxonomic diversity (number of taxa preserved). Other analyses are needed to complete the picture such as morphological disparity, which is a particularly useful tool. By looking at changes in conch

morphology over time researchers are able to test hypotheses about the severity and nature of extinction events.

Taxonomic diversity is often independent of morphological disparity, and because of this morphological disparity can help to mitigate the sampling bias of the fossil record. By focusing on differences in shape of the ammonoid conchs, morphological disparity can achieve a degree of independence from taxonomy. It is this independence that makes it possible to compare samples with varying degrees of taxa, which is obviously not possible if one only uses taxonomic diversity. Disparity analyses consider the spread of taxa and the areas of occupied morphospace occupied during successive time intervals.

The Ammonoidea are excellent candidates for analyzing extinction dynamics. They show a wide variability in their taxonomic diversity over time and they survived many extinction episodes. The diversity dynamics of ammonoids analyzed by the distribution patterns of over 4000 species obtained from the AMMON database and ranging from the Emsian stage (Early Devonian) to the Triassic gives us a deep insight into the evolutionary history of the clade.

The results of these analyses allowed for a comparison of the effects of extinction events as well as subsequent radiations. It turned out that only the Kellwasser Events, the Hangenberg Event and the Permian-Triassic Event had major effects on the ammonoid morphospace. The end-Eifelian Kačák Event had a more intense effect than the end-Givetian Taghanic Event. Due to the complex nature of ecosystems and how they are brought towards a point of collapse, it would be unlikely that these events all had identical courses, causes and effects. The Hangenberg Event was the most severe of the Paleozoic extinctions for the Ammonoidea, because all but one group became extinct. Despite more than one group surviving the other events, however, only one clade would last long enough to provide the rootstock for subsequent ammonoid evolution. The other clades can be considered as cases of 'dead clades walking'. The random reduction in morphospace that occurs at some of the events (e.g., end-Permian) would indicate that they were non-selective in nature in terms of conch morphology. In contrast, the Kellwasser and Hangenberg extinctions were morphologically selective, with distinct forms preferentially eliminated (e.g., Korn et al. 2013b).

The extinction-processes during the Paleozoic seem to have differed. However, due to preservational and sampling biases ('Signor-Lipps effect': Signor and Lipps 1982) this is hard to assess. Bearing this in mind, current data would indicate that the Kačák and Hangenberg Events occurred rather suddenly, but the end-Permian and the end-Frasnian events were played out over longer periods of time in a more stepwise fashion.

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